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Larval Growth and Metamorphosis of *Conus* (Gastropoda: Toxoglossa) in Hawaii[1]

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ABSTRACT: The planktotrophic larvae of *Conus lividus*, *C. quercinus*, *C. flavidus*, *C. striatus*, and *C. marmoreus* were reared through metamorphosis in the laboratory and were described and figured. Minimum planktonic periods of these species were found to be 50, 30, 23, 20, and 10 days, respectively. The lecithotrophic larvae of *C. pennaceus* metamorphosed within 24 hours of escape from their egg capsules. Early post-hatching growth rates of planktotrophic veligers were related to hatching size and the developmental state of the velum at hatching. In *C. pennaceus*, metamorphosis was induced by the presence of a biological film. Substratum texture had no effect on rates of metamorphosis. The lecithotrophic larvae of *C. pennaceus* were observed to ingest unicellular algae. Experiments showed that this facultative feeding may improve the survival of *C. pennaceus* when the larval period is artificially prolonged.

GASTROPODS IN THE GENUS *Conus* are important and conspicuous components of tropical coral reef ecosystems. Although extensive ecological research has been carried out on populations of adult *Conus* (Kohn 1959, Kohn and Nybakken 1975, Leviten 1974), little work has been done on the early life histories of these mollusks. Information on the larval biology of benthic marine invertebrates is important because the large and small scale distribution patterns of these species are often determined to a large extent by the dispersal potential and site-specificity at recruitment of their larvae. Scheltema (1961, 1971) and Hansen (1978) have commented on the impact of larval biology on the distribution of gastropod species in space and time respectively, and Kohn and Leviten (1976) have suggested that patterns of larval settlement may have an effect on the population density and species diversity of *Conus* assemblages. This paper will describe laboratory rearing studies on the larvae of 6 species of *Conus* and present the results of experiments on the larval settlement and metamorphosis of *C. pennaceus*.

The vast majority of tropical gastropod species have planktotrophic larvae which must feed in the plankton before settling and metamorphosing in the benthic environment (Thorson 1946). The necessity of finding the correct food for planktotrophic larvae has frequently discouraged laboratory cultivation of these species (Berg 1972, Kohn 1961*a*). Recently, however, Scheltema (1962) and others have developed rearing techniques that are applicable to a wide variety of gastropod larvae.

Perron (1980) successfully reared the planktotrophic larvae of *Conus textile* using a modification of the techniques devised by Brownell (1977), and additional data on *Conus* comparative larval biology are presented by Perron (1981*a*). Information on the intracapsular development of *Conus* embryos has been contributed by Ostergaard (1950), Natarajan (1957), Kohn (1961*a*,*b*), Nybakken (1970), Bandel (1976), Cruz, Corpuz, and Olivera (1978), and Perron (1981*b*). Taylor (1975) has identified, described, and figured the planktonic larvae of 9 species of Hawaiian *Conus*.

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METHODS

Adult specimens of *Conus pennaceus*, *C. marmoreus*, *C. striatus*, *C. quercinus*, *C. flavidus*, and *C. lividus* were kept in tanks of flowing seawater at the Kewalo Marine Laboratory of the Pacific Biomedical Research Center in Honolulu. Egg capsules were obtained from animals maintained in the laboratory or were collected from reefs around the island of Oahu by SCUBA diving or snorkeling.

The larvae of most species were reared in 55-l fiberglass tanks according to the techniques that proved successful for *Conus textile* (Perron 1980). However, the larvae of *C. lividus* survived best when reared in 2-l glass beakers. All larvae were fed a mixed phytoplankton culture made up of equal volumes of *Isochrysis galbana* and *Phaeodactylum tricornutum*. Larval shell growth and dry weight increase was monitored by removing larvae from cultures at regular intervals. These larvae were then measured under a microscope equipped with an ocular micrometer, dried to constant weight, and individually weighed to the nearest .001 mg on a Cahn 25 electrobalance. For larvae of each species, starved control cultures were kept in seawater passed through a Millipore filter (1.2 μm pore size). For all species except *C. marmoreus*, starved control cultures contained mixed antibiotics (Penicillin G and Streptomycin sulfate at 60 μg and 50 μg/ml, respectively) (Switzer-Dunlap and Hadfield 1977).

Conus larvae were observed to metamorphose spontaneously on the fiberglass sides of the 55-l rearing tanks or, in the case of *C. lividus*, on rocks added to their glass rearing beakers. Since larvae seldom metamorphosed on clean glass surfaces, it was deduced that the biological film on the rearing tank walls and/or the rough texture of the fiberglass itself served as the metamorphic inducer. Metamorphosis experiments were run on the larvae of *C. pennaceus*. Since the larvae of this species can metamorphose within a few hours of escape from their egg capsules, metamorphically competent larvae could be conveniently obtained for replicated experiments.

Experiments designed to test the relative importance of substratum texture and chemical characteristics were run with 100 larvae per trial. In each trial, 25 larvae were subjected to one of 4 treatments and numbers of metamorphosed larvae were counted after 24 hours on each of the 4 substrata tested. The 4 treatments were: acid cleaned glass bowls, glass bowls with biological films, acid cleaned volcanic rocks, and rocks with biological films. Millipore-filtered seawater was used in all trials, and biological films were obtained by leaving bowls and rocks in flowing seawater for 48 hours. Eight separate trials of 4 treatments each were run using a total of 800 *C. pennaceus* larvae. Results were analyzed using chi-square tests.

Aspects of the nutritional requirements of *Conus pennaceus* larvae were also examined in this study. The importance of intracapsular fluid to the nutrition of developing embryos was assessed by removing early stage embryos from their capsules and rearing them without intracapsular fluid. In these experiments, late gastrula stage embryos were placed in finger bowls with Millipore-filtered, antibiotic-treated seawater. Three bowls of 50 embryos each were examined. Each bowl contained embryos from egg masses of a different parent. Control embryos, in unopened capsules, were maintained in Millipore-filtered, antibiotic-treated seawater and were monitored throughout the experiment until natural hatching of fully developed larvae took place. Experimental and control larvae were then measured and tested for ability to undergo metamorphosis.

The importance of facultative planktotrophic feeding to the lecithotrophic larvae of *Conus pennaceus* was examined by maintaining starved larvae and larvae fed the unicellular alga *Isochrysis galbana* in glass bowls over long periods of time. Each fed or starved culture contained 25 larvae. Cultures were changed daily and records of cumulative mortality were kept until all larvae had died. The experiment was repeated 4 times

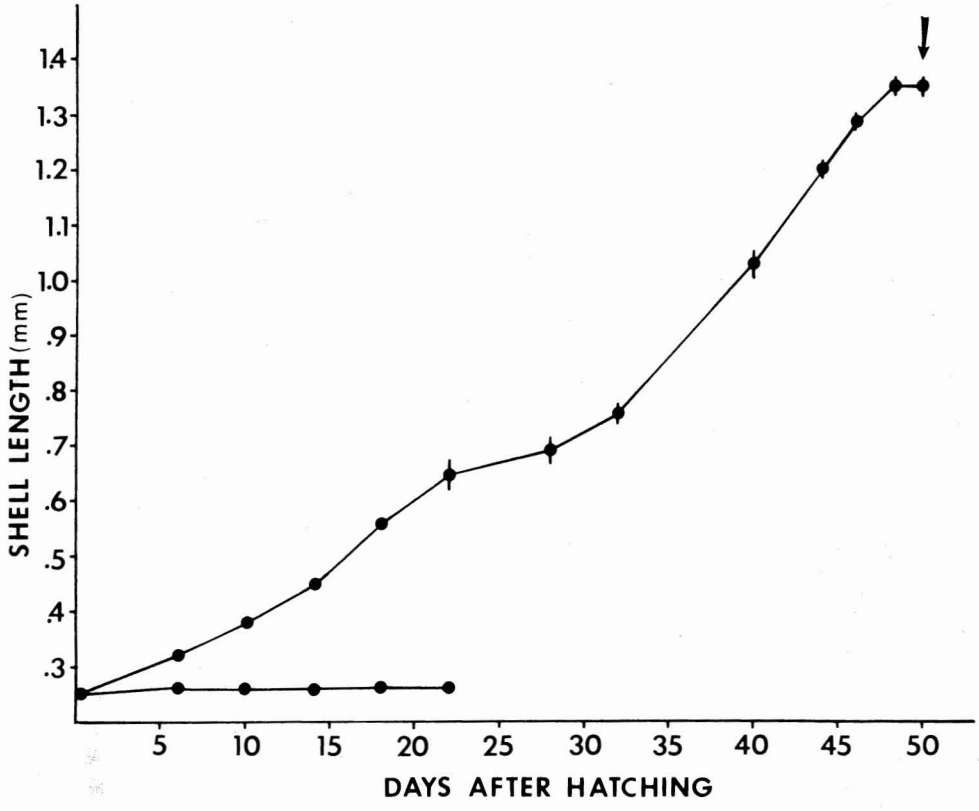

FIGURE 1. The growth of fed (top curve) and starved (bottom curve) *Conus lividus* larvae. Each dot is the mean shell length of 10 larvae. Error bars indicate 1 SD. Arrow indicates metamorphosis.

with larvae from different parents. The effect of facultative planktotrophic feeding on the ability to metamorphose and on postmetamorphic survival of *C. pennaceus* juveniles was similarly determined. Fed and starved larvae were maintained in clean glass bowls for 20 days after hatching before being placed in bowls with biologically conditioned rocks. Numbers of metamorphosed larvae were counted after 24 hours. The metamorphosed juveniles were then kept in filtered seawater, without food, until all had died. In this way, differences in survival of starved postmetamorphic juveniles could be related to the nutritional history of premetamorphic larvae. This experiment consisted of 7 trials of 50 larvae each (25 starved and 25 fed). In the *C. pennaceus* feeding experiments, differences in mortality between fed and starved cultures were analyzed using Mann-Whitney tests.

RESULTS

The growth curves of the planktotrophic larvae of *Conus lividus*, *C. flavidus*, *C. striatus*, and *C. marmoreus* are presented in Figures 1–4. Each curve is accompanied by data on the growth and survival of starved larvae. For each of these species except *C. lividus*, increase in larval dry weight is plotted along with increase in shell length. No growth curve is presented for *C. pennaceus* because this species shows no shell growth during the brief period between hatching and metamorphosis. The larvae of *C. quercinus* were reared to metamorphosis

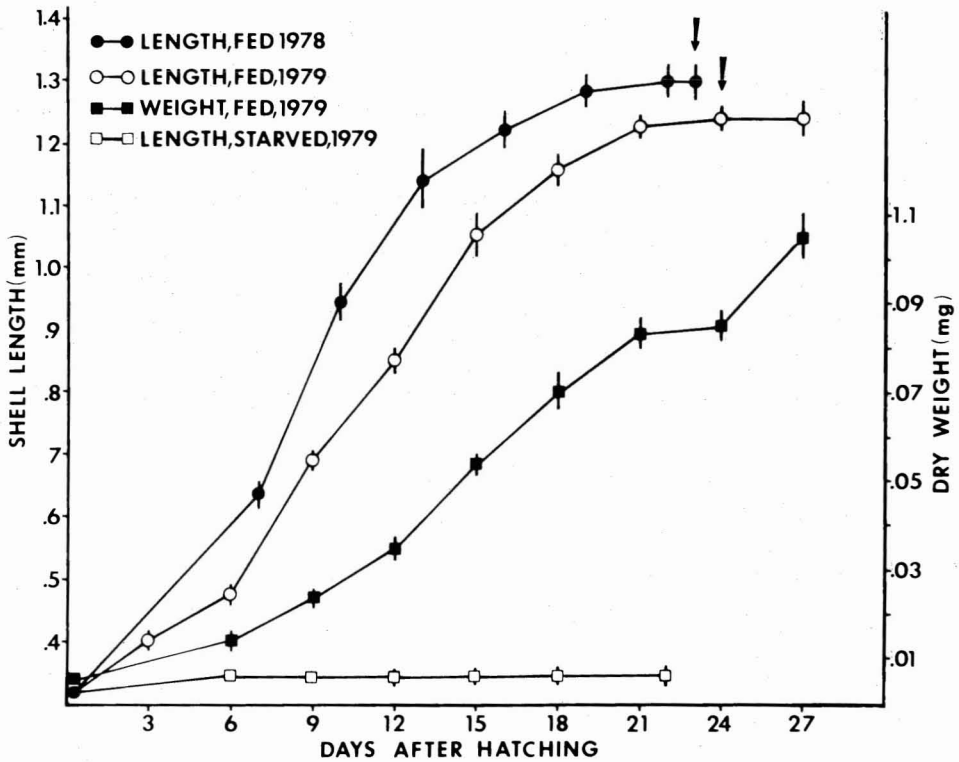

FIGURE 2. The growth in length and dry weight of fed and starved *Conus flavidus* larvae.

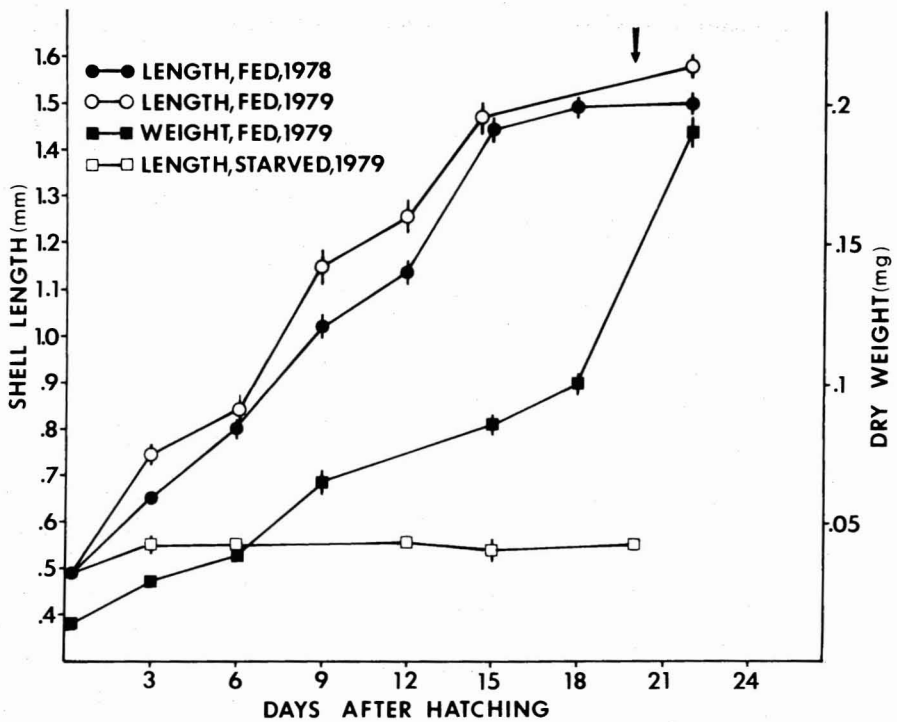

FIGURE 3. The growth in length and dry weight of fed and starved *Conus striatus* larvae.

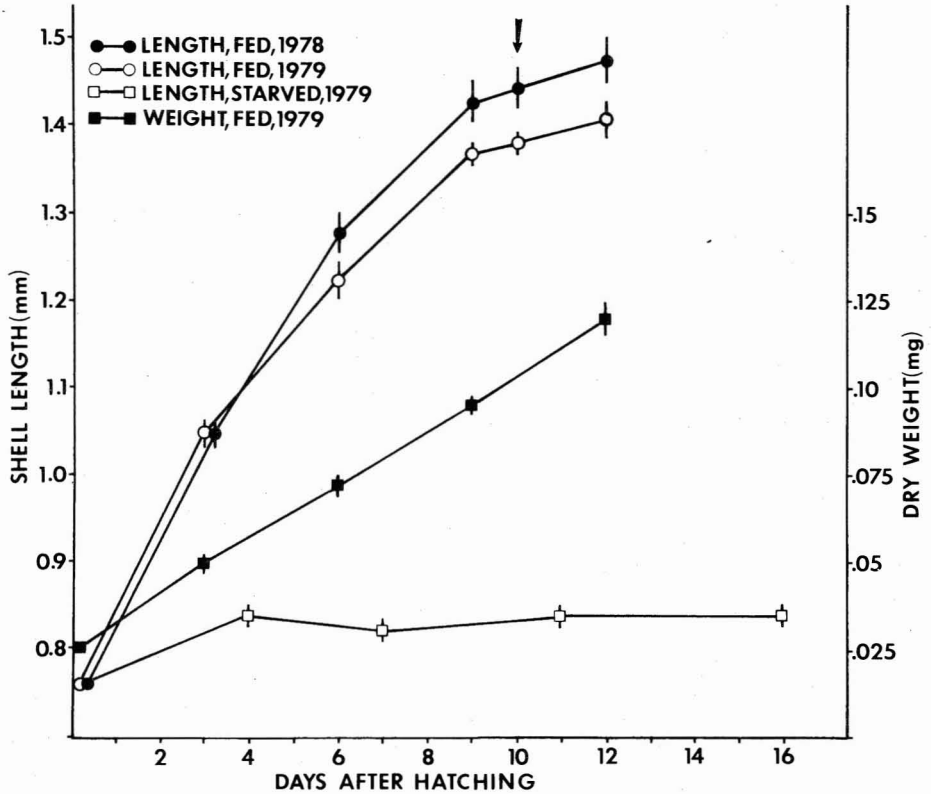

FIGURE 4. The growth in length and dry weight of fed and starved *Conus marmoreus* larvae.

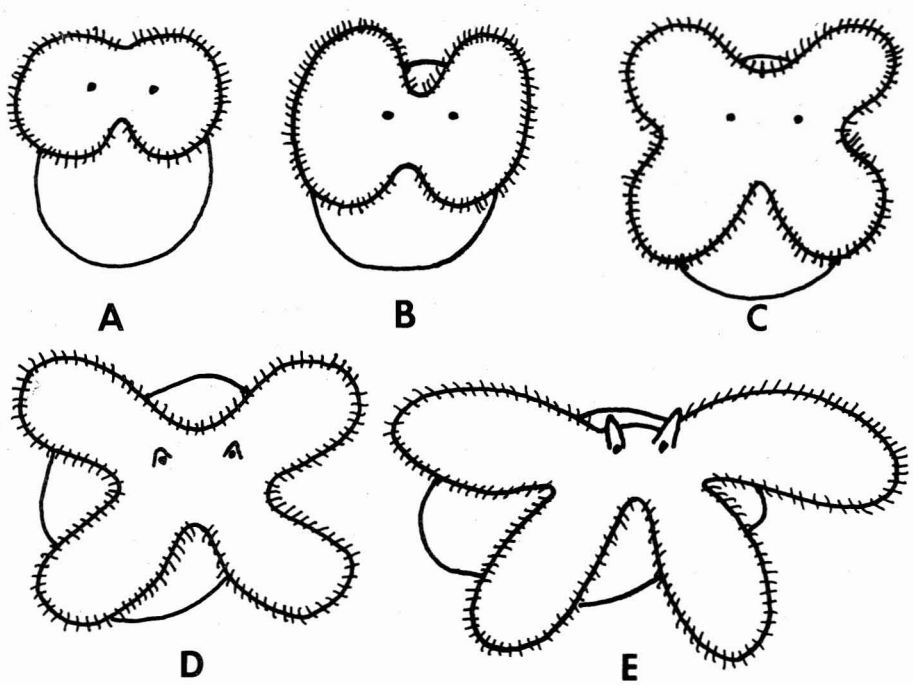

FIGURE 5. Stages of velum development in *Conus* larvae. The series of diagrams from *A–E* represents the ontogeny of the velum in *C. lividus*. The diagrams also represent the hatching stage larvae of the following species: *A*, *C. lividus*; *B*, *C. flavidus*; *C*, *C. striatus*; *D*, *C. marmoreus*; *E*, *C. pennaceus*. The diagrams are not all drawn to the same scale.

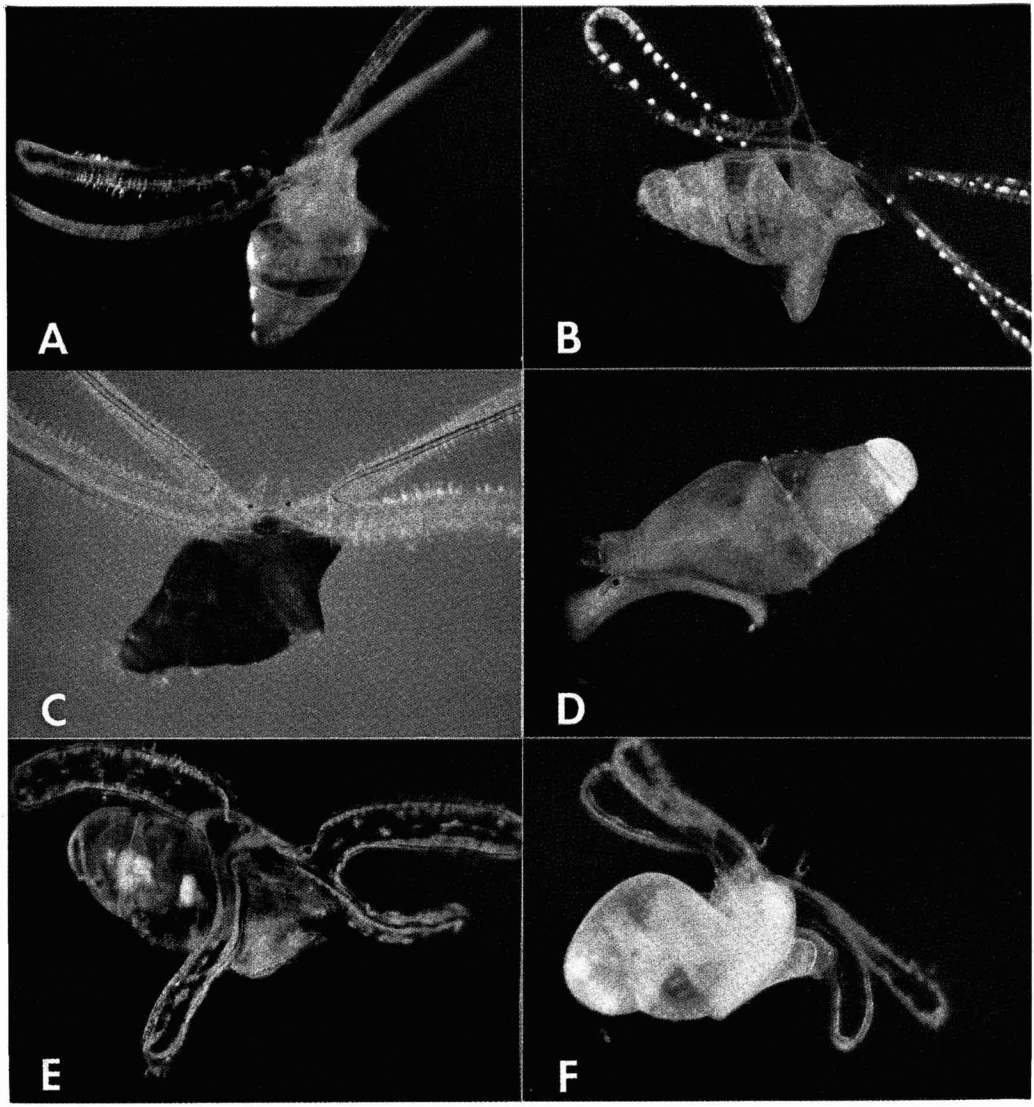

FIGURE 6. Photomicrographs of the fully developed veliger larvae of *A*, *C. lividus*; *B*, *C. flavidus*; *C*, *C. quercinus*; *E*, *C. marmoreus*; *F*, *C. pennaceus*. *D* is the newly metamorphosed juvenile of *C. striatus*.

but no data on growth were obtained for this species.

There are no data to suggest that *Conus* embryos derive significant nutrition from intracapsular fluid before hatching. The embryos of *C. pennaceus*, raised without intracapsular fluid, attained hatching sizes insignificantly different from those of encapsulated controls ($t = 0.75$, $df = 98$). When placed on biologically conditioned rocks, 92 of 96 artificially reared larvae metamorphosed within 24 hours. The embryos of *C. lividus* and *C. quercinus* also appeared to develop normally after removal from capsules at the blastula stage. Since the embryos of *C. pennaceus* remain in their egg capsules longer than those of any other Hawaiian species of *Conus* (Perron 1981*a*), this species is the most likely to obtain nutrition from intracapsular fluid.

TABLE 1

SURVIVAL OF STARVED AND FED *Conus pennaceus* LARVAE

	SURVIVAL IN DAYS AFTER HATCHING			
	FED		STARVED	
COHORTS	50% MORTALITY	100% MORTALITY	50% MORTALITY	100% MORTALITY
1	31	39	29	30
2	33	37	25	27
3	34	38	24	30
4	30	35	25	27
$\bar{x}$	32	37	26	29

NOTE: Survival is measured in numbers of days to 50% and 100% mortality in cultures. Mann-Whitney tests show significant ($P = 0.05$) differences in time to both 50% and 100% mortality between starved and fed cultures.

Between hatching and metamorphosis, planktotrophic *Conus* larvae followed a characteristic pattern of growth and development that varied from species to species as a function of hatching size. Other than the growth of the larval shell, the most obvious developmental process that took place during planktonic life was the ontogeny of the velum, the larval gastropod's swimming and feeding organ (Figure 5). Of the species examined in the present study, *C. lividus* had the smallest hatching size (Figure 1), and emerged from the egg capsule with a simple bilobed velum (Figure 5*A*). The rounded velar lobes slowly enlarged (Figure 5*B*) and began to bifurcate a week or more after hatching (Figure 5*C*). Further enlargement of the velum took place (Figures 5*D*, *E*) until a fully developed veliger larva was formed (Figure 6*A*).The larvae of the other species of *Conus* went through similar stages of velum development. However, as hatching size increased among these species (Figures 2–4), so did the developmental state of the velum at hatching. *Conus flavidus* larvae hatched with a pair of rounded velar lobes (Figure 5*B*) which began to bifurcate a day or two later, while C. *striatus* and *C. marmoreus* hatched with well bifurcated velar lobes (Figures 5*C*, *D*). The lecithotrophic larvae of *C. pennaceus* hatched as fully formed veligers (Figures 5*E*, 6*F*). Thus, Figure 5 shows both the basic pattern of velum ontogeny in larvae of the genus *Conus* and the developmental state of the velum at hatching in the various species examined.

Maximum survival times of starved newly hatched larvae are given in Figures 1–4 for the planktotrophic species and in Table 1 for *Conus pennaceus*. The relatively short survival times of starved *C. marmoreus* larvae may have been because cultures of this species were not treated with antibiotics. Although starved *C. pennaceus* larvae survived for up to 30 days after hatching, this figure may not be comparable with those for the planktotrophic species. While the early larvae of the planktotrophic species swam actively in culture, those of *C. pennaceus* rested on the bottom of the culture vessel and were relatively inactive.

While shell growth of fed planktotrophic larvae tended to level off just prior to metamorphosis, dry weight continued to increase (Figures 2–4). In *Conus flavidus* and *C. striatus* the rate of dry weight gain increased just after metamorphosis. In these two species, metamorphosis was accompanied by a marked change in pigmentation of the larval shell.

The photomicrographs in Figure 6 are presented both to illustrate the diversity of *Conus* veliger larvae and to aid in the identification of larvae and postmetamorphic juveniles by future workers.

Conus lividus

Figures 6*A*, 7*A*

The veliger larva of *C. lividus* has a bright yellow shell and measures 1.38 mm in maximum length at settling. Since the hatching

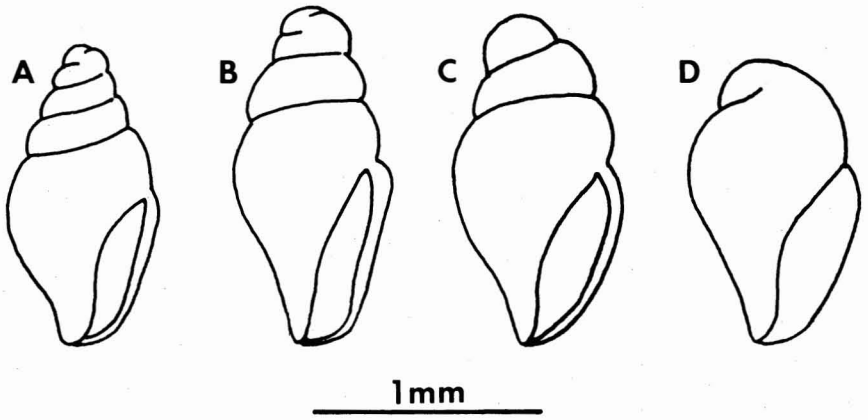

FIGURE 7. The larval shells of *A*, *C. lividus*; *B*, *C. striatus*; *C*, *C. marmoreus*, and *D*, *C. pennaceus*.

shell is only 0.25 mm in diameter, the apex of the fully developed veliger shell is correspondingly delicate and pointed. After metamorphosis, purple pigment spots appear at the growing edge of the juvenile shell.

C. flavidus

Figure 6*B*

The larval shell of *C. flavidus* is nearly colorless, but rapidly develops a uniform purple pigmentation after metamorphosis. The hatching shell measures 0.32 mm while the fully grown larva settles at 1.23 mm in length.

C. quercinus

Figure 6*C*

The larvae of *C. quercinus* are among the most distinctive of all the pelagic *Conus* larvae in Hawaii. The shell is chestnut brown while the velum is densely lined with yellow pigment spots. The larvae hatch at 0.28 mm and settle at an average length of 1.33 mm (Perron 1981*a*).

C. striatus

Figures 6*D*, 7*B*

In this study, the larvae of *C. striatus* metamorphosed at a mean shell length of 1.52 mm. The color of the larval shell is faintly pink until metamorphosis when it turns a bright orange (Figure 6*D*). Since the hatching size of *C. striatus* is 0.49 mm, the apex of the larval shell is blunt in comparison to that of *C. lividus*.

C. marmoreus

Figures 6*E*, 7*C*

Hatching at a shell length of 0.75 mm, the larva of *C. marmoreus* has an even blunter apex than that of *C. striatus*. Although the larval shell of *C. marmoreus* is only faintly yellow in color, the brown internal organs show through the transparent shell. Metamorphosis takes place at an average shell length of 1.48 mm.

C. pennaceus

Figures 6*F*, 7*D*

The larvae of *C. pennaceus* could hardly be mistaken for those of any other species of Hawaiian *Conus*. Although *C. pennaceus* larvae are weak swimmers and usually metamorphose within hours of hatching, they may occasionally be swept up by currents and carried into the plankton. The larval shell is extremely blunt with a reduced number of whorls. Larval shell color may be white, orange, or purple. Although a single *C. pennaceus* egg capsule may contain all three color types, local populations of this species are often characterized by a preponderance of one color form. The average

TABLE 2

EFFECT OF SUBSTRATUM TEXTURE AND CHEMISTRY ON THE METAMORPHIC RESPONSE OF *Conus pennaceus* LARVAE

	BIOLOGICAL FILM		
TEXTURE	PRESENT	ABSENT	TOTAL
Rough	162	28	190
Smooth	172	18	190
Total	334	46	

NOTE: Each row and column figure in the contingency table represents the number of larvae metamorphosing out of 8 trials of 25 larvae each.

hatching and settling size of *C. pennaceus* larvae is 1.25 mm.

Metamorphosis of all the *Conus* species examined in the present study appeared identical to that of *C. textile* (Perron 1980), with resorption of the velum being the most obvious morphological change. Minimum pelagic periods of *C. lividus*, *C. quercinus*, *C. flavidus*, *C. striatus*, and *C. marmoreus* were 50, 30, 23, 20, and 10 days, respectively, while the larvae of *C. pennaceus* metamorphosed within 24 hours of hatching.

Table 2 presents the results of experiments designed to determine which substratum characteristics are most effective in inducing the metamorphosis of *Conus* larvae. The results of tests on 800 *C. pennaceus* larvae show that the presence of a biological film was sufficient to stimulate metamorphosis in 83 percent of the larvae tested. By contrast, metamorphosis was observed in only 12 percent of the larvae placed on biologically "clean" substrata. These differences were highly significant when subjected to a chi-square test. The data in Table 2 also show that substratum texture does not significantly influence rates of metamorphosis, and a chi-square test of independence (Sokal and Rohlf 1969) reveals no significant interaction between substratum texture and chemistry ($\chi^2 = 2.4$, $P \gg 0.1$).

The larvae of *Conus pennaceus* are lecithotrophic in that they can attain metamorphic competence without utilizing an external food source. However, if *C. pennaceus* larvae are placed in water containing the unicellular alga *Isochrysis galbana*, the larvae soon accumulate algal cells in their stomachs, and their previously colorless digestive glands turn a bright green. Table 1 shows the results of experiments designed to test the effect of this facultative feeding on the survival of *C. pennaceus* larvae. Larvae kept in biological "clean" glass bowls to prevent metamorphosis survived significantly longer when fed *I. galbana* than when starved in Millipore-filtered seawater. Differences were significant whether survival was measured in terms of time to 100 percent mortality ($P = 0.05$) or time to 50 percent mortality ($P = 0.05$) (Mann-Whitney tests).

The results of experiments on the effect of facultative feeding on metamorphic success and subsequent postlarval survival were less conclusive. Groups of fed and starved *Conus pennaceus* larvae kept in clean glass bowls for 20 days after hatching metamorphosed at rates of 82.7 percent and 83.9 percent, respectively, when placed on biologically conditioned surfaces. Table 3 shows the survival times of these metamorphosed juveniles during subsequent starvation trials. When subjected to Mann-Whitney tests, differences in survival between starved and fed animals were nonsignificant ($P > 0.05$).

DISCUSSION

The veliger larvae of 15 Hawaiian species of *Conus* have now been described and figured. Taylor (1975) provided drawings and/or photographs of the fully developed larvae of *C. vitulinus*, *C. striatus*, *C. sponsalis*, *C. rattus*, *C. pulicarius*, *C. obscurus*, *C. pertusus*, *C. vexillum*, and *C. abbreviatus*. The present study contributes photographs of the larvae of *C. lividus*, *C. flavidus*, *C. quercinus*, and *C. marmoreus* (Figure 6). The larvae of *C. pennaceus* and *C. textile* have been figured by Ostergaard (1950) and Perron (1980), respectively.

The larvae of Hawaiian species of *Conus* range in shell length at settling from 1.12 mm for *C. abbreviatus* to 2.15 mm for *C. pertusus* (Taylor 1975). Although Taylor lists

TABLE 3

EFFECT OF FACULTATIVE PLANKTONIC FEEDING ON POSTMETAMORPHIC SURVIVAL OF STARVED *Conus pennaceus* JUVENILES

SURVIVAL IN DAYS AFTER METAMORPHOSIS			
FED		STARVED	
50% MORTALITY	100% MORTALITY	50% MORTALITY	100% MORTALITY
15(3–25)	24(22–29)	12(8–23)	20(14–26)

NOTE: Values are means and total ranges. Mann-Whitney tests show no significant differences in time to 50% or 100% mortality between starved and fed cultures.

the settling size of *C. striatus* as 2.5 mm, I believe that this figure is in error. In the present study, *C. striatus* larvae metamorphosed spontaneously at an average shell length of 1.52 mm. Also, Taylor's (1975) drawing of "*C. striatus*" has an apical whorl which appears too small in diameter for a *Conus* larva hatching at just under 0.50 mm in shell length. Finally, I measured protoconchs of juvenile *C. striatus* collected in the field and, using the techniques described by Perron (1980), estimated settling sizes of approximately 1.5 mm.

The series of *Conus* larvae examined in this study provides a clear demonstration of how protoconch characteristics can reveal other aspects of larval biology within a taxon. The "shell apex theory," as originally formulated by Thorson (1950) and recently reviewed by Jablonski and Lutz (1980), states that a clumsy, large apex points to nonpelagic development while a delicately pointed apex indicates pelagic development. Within closely related groups, this rule is generally reliable and has been used to estimate developmental types of fossil gastropod species (Hansen 1980, Shuto 1974). The results of the present study suggest that the diameter of the apical protoconch whorl may be used to predict not only basic developmental type, but also the relative durations of minimum planktonic periods in species with pelagic larvae. The apex of the fully developed veliger shell constitutes the shell of the hatching-stage larva. In *Conus*, this hatching-stage shell, also known as *Protoconch I* (Fretter 1967), can be distinguished from the remainder of the larval shell (*Protoconch II*). In some *Conus* species, *Protoconch I* turns white at metamorphosis is contrast to the pigmentation of *Protoconch II* (Figure 6*D*). Since there is a highly significant correlation between hatching size and minimum planktonic period in *Conus* species (Perron 1981*a*), it follows that apical whorl or *Protoconch I* sizes should be good estimators of the minimum periods that larvae remain in the plankton before metamorphosis.

Although the minimum planktonic periods of the pelagic Hawaiian *Conus* larvae studied here vary from 10 to 50 days, the limited growth and survival of starved control cultures (Figures 1–4) demonstrate that all of these species are obligatorily planktotrophic. With the exception of the nonpelagic lecithotrophic larvae of *C. pennaceus*, the maximum survival times of starved hatching-stage larvae do not appear to be correlated with size at hatching. However, previous workers have assumed that small larvae are more susceptible to starvation than are large ones (Vance 1973). In the present study, the three species whose larvae were starved in antibiotic-treated Millipore-filtered seawater had hatching sizes ranging from 0.25 mm to 0.49 mm (Figures 1–3). Since starvation times ranged from 19 to 22 days with the longest surviving larvae having the smallest hatching sizes, the data do not support the hypothesis that resistance to planktonic starvation is positively related to larval size. The failure of large larvae to outlive small ones under starvation conditions may be due to increased energy costs of swimming in larger and heavier larvae. The extended survival of

C. pennaceus larvae (Table 1) may result from the reduced swimming activity of these essentially nonpelagic larvae.

Conus pennaceus is the only species of Hawaiian *Conus* known to have lecithotrophic larvae. The data in the present study indicate that these larvae rely only on stored yolk reserves during the entire course of their premetamorphic development. Although Natarajan (1957) claimed that the lecithotrophic larvae of the Indian Ocean species *C. araneosus* feed on intracapsular albumin before hatching, he presented no data in support of this idea.

Between hatching and metamorphosis, *Conus pennaceus* larvae are capable of feeding on unicellular algae. Experimental results presented here show that when the larval period is artificially prolonged, the viability of *C. pennaceus* is enhanced by facultative planktotrophic feeding (Table 1). Larval feeding may also have a small effect on postmetamorphic survival of *C. pennaceus* juveniles (Table 3). However, since *C. pennaceus* larvae normally settle within a few hours of emergence from the egg capsule and will metamorphose on virtually any marine surface with a biological film (Table 2), it is doubtful that facultative planktotrophic feeding has a significant effect on their survival in nature. Nevertheless, it is possible that larvae of this species are sometimes carried into surface waters by swift currents and maintained afloat by turbulence acting on the outstretched velum. Under such conditions, the pelagic period could be extended and facultative planktotrophic feeding may increase the likelihood of survival until a favorable substratum is encountered. On the other hand, the ability to ingest and utilize phytoplankton may represent the retention, in vestigial form, of the feeding characteristics of a planktotrophic ancestor.

It is generally believed that the larval form of the ancestral gastropod was a planktotrophic veliger (Jagersten 1972). The basic developmental pattern of *Conus* larvae (Figure 5) and the inverse relationship between hatching size and pelagic period (Figures 1–4) suggest that the primitive *Conus* larval form was a long-term planktotroph with a small hatching size and a simple velum at hatching (Figure 5*A*). Hawaiian species of *Conus* such as *C. lividus*, which have small hatching sizes and long planktonic periods, pass through developmental stages that are homologous with the hatching stages of species like *C. striatus* and *C. marmoreus*, which hatch at larger sizes and spend shorter periods of time in the plankton. This trend reaches its logical conclusion with *C. pennaceus*, which hatches as a fully developed veliger larva ready for metamorphosis.

Size and developmental state of the velum at hatching appear to be correlated with post-hatching planktonic growth rate in planktotrophic species of *Conus* (Figures 1–4, Perron 1981*a*). The food-gathering capacity of the velum is related to the length of the ciliated groove that runs around the perimeter of each velar lobe (Strathmann 1978). As the velum enlarges and especially as velar lobe bifurcation takes place (Figure 5*C*), the effective length of the food-gathering filter increases.

As *Conus* veliger larvae approach metamorphic size, growth rate decreases and remains relatively depressed until at least a few days after metamorphosis (Figures 1–4). Perron (1980), working with the larvae of *C. textile*, found that although the rate of shell-length increase dropped off at metamorphosis, the rate of dry-weight increase accelerated. This phenomenon was also observed in the metamorphosing larvae of *C. flavidus* and *C. striatus*. In the case of *C. marmoreus*, dry weight continued to increase linearly while shell growth slowed. Since newly metamorphosed larvae are no longer feeding on phytoplankton and have not yet begun feeding on their adult prey, the increase in dry weight is probably the result of shell calcification or thickening. The increase in dry weight of *C. striatus* and *C. flavidus* larvae at metamorphosis is paralleled by a dramatic change in shell pigmentation. A similar color change was noted in the metamorphosing larvae of *C. textile* by Perron (1980), who suggested that while a light shell is advantageous to a swimming veliger, a heavier, stronger shell may be useful upon recruitment into the benthic environment where

many predators are adapted for crushing shelled prey.

Recruitment and metamorphosis mark one of the more critical and dangerous phases in the life cycles of benthic marine invertebrates. Although metamorphosis involves profound morphological changes, many of which have been studied in a variety of opisthobranch (Bonar and Hadfield 1974, Thompson 1958) and prosobranch gastropods (D'Asaro 1965, Fretter 1969), the emphasis of the present study is ecological. Specifically, we wish to know if the spatial distribution of adult animals can be explained as a function of site-specific larval recruitment. In general, gastropod species that feed on a narrow range of patchily distributed food types will metamorphose only in the presence of the appropriate food species (Hadfield 1978 and references therein). The spatial distribution of adults of these gastropod species is clearly related to specific "choices" made by larvae at metamorphosis. On the other hand, species that are omnivorous or utilize an abundant food source may metamorphose in response to less specific stimuli (Brownell 1977, Heslinga 1981, Scheltema 1961). In the present study, *Conus* larvae of several species readily metamorphosed on biologically conditioned rocks, coral, fiberglass, and laboratory glassware. Since acid-cleaned surfaces are rare in the marine environment, the *Conus* settling response must be described as generalized. Therefore, the available data do not support the idea that settlement sites of *Conus* larvae are located by highly specific chemical discrimination between alternative substrata. Although *Conus* species are known to have rigid prey preferences (Kohn 1959), the lack of highly specific metamorphic induction in the genus may be explained by the observation that *Conus* prey species are abundant on intertidal benches (Leviten 1974) and are probably not patchily distributed on the reef.

Leviten (1974) and Kohn and Leviten (1976) have shown that abundant refuges (rubble-filled depressions and algal mats) enhance *Conus* species richness and population density on marine benches. These workers have also suggested that the refuges may serve as settling sites for *Conus* veliger larvae. Although the data on *Conus* metamorphic responses indicate that larvae are not likely to be specifically attracted to refuges, other processes could result in the accumulation of juveniles in sheltered sites. Larvae settling on exposed portions of marine benches may be dislodged by wave action and moved about at random until an algal mat or rubble-filled depression is encountered. Since settling larvae usually crawl about the substratum for several minutes before beginning metamorphosis, larvae settling near refuges could locate these sites during this brief period of exploration (Crisp 1977). Another possibility is that larvae settling in refuges may enjoy higher postmetamorphic survival rates than those settling on exposed surfaces. Finally, early postmetamorphic juveniles may actively seek out sheltered sites (Kohn and Leviten 1976). It therefore appears doubtful that the spatial distribution of adult *Conus* on marine benches is entirely explainable in terms of larval biology. However, major differences in habitat between species could be maintained by gross differences in larval behavior. For example, the larvae of species that live in deep-water habitats may become photonegative and swim to the bottom coincident with the attainment of metamorphic competence. Intertidal bench species, on the other hand, may not become photonegative until they have been washed into turbulent shallow water.

The tentative nature of the foregoing conclusions clearly indicates the need for further research on *Conus* larval biology. At present, larvae have been described for roughly half of the common Hawaiian species of *Conus*, and data on planktonic periods are available for 8 species. Although the data are incomplete, we know more about *Conus* life histories than about those of any comparable tropical gastropod taxon. Additional research on *Conus* larval biology and further emphasis on the integration of studies on adult and larval ecology should increase our understanding of the complex ecological interrelationships within coral reef communities.

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